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THE AMERICAN NATURALIST

VOL. L.

July, 1916

No. 595

SEX CONTROL AND KNOWN CORRELATIONS IN PIGEONS¹

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WHEN one nowadays states that he has obtained a real control—a reversal—of the development of sex, he can feel assured that his biological audience demands a very large volume of rigid proofs. The first reason for this large requirement is, as you well know, that the assertion of sex control has been often made, and that in most of these cases the data have proved disappointing; inadequate in one or another respect. A second reason for present widespread skepticism as to even the possibility of a real control of sex-development centers in the now well-demonstrated fact that in some groups of animals, the male—and in other cases the female—produces sex cells of two kinds when these are considered from the standpoint of their chromosomal numbers or characteristics; and further that each of these two groups of germs *normally* gives rise to organisms of the sex corresponding to the chromosomal constitution of these germs. Moreover, certain linkage phenomena observed in breeding such forms, unquestionably show themselves to be *normally* associated with these same chromosomal differences.

But the experimentalist has learned through some pre-

¹ Paper read before the American Society of Naturalists, Columbus, Ohio, December 30, 1915.

vious contests with ideas of fixity and causality that when *normal* structural correlations have been demonstrated in the field of development, *nothing* has been decided as to *causality* and *inflexibility*; indeed it is commonly at such a point that experiment applies the pressure of *new* or *unusual* conditions and makes an approach toward learning the nature of a phenomenon, by forcing the latter to break from its normal correlations, and disclose something of its real nature through its versatility—through its own capacity to shift from response to one set of conditions, to response to another set of conditions. Laws of causation, in the field of development, are not to be deduced from studies concerning the normal associations of the *structures* of the cell; they may be approached through demonstrations of the versatility and responsiveness under pressure of those *processes* native to living matter.

We have stated that when sex is controlled an audience like this will demand a volume of proof. It is clear that the time limits here do not admit so extensive a presentation. I should like to note here, however, that Professor Whitman's complete studies on sex in doves and pigeons have been prepared for publication, and for several months have been in the hands of the publisher. The results of my own studies of the past five years designed to test the reality of the sex-control, and the nature of sex, as exhibited in these forms, will already doubtless fill another volume. And, since the last volume of the posthumous works of Professor Whitman is nearing completion, I can promise that it will not be long before the work of preparing my own results for publication will be begun. Only when all of these data are fully available to you, may we expect a judgment as to whether the evidence for our thesis to-day is adequate. It is possible to give here, within the time limits, only an outline of the *kinds of study* which have yielded evidence on the question of sex-control in pigeons.

These studies were begun, and carried on for many years by Professor Whitman. He obtained indispu-

tably—a profound modification of the sex-ratio, and identified in a general way the factors associated with the modified ratios. Whether the modified ratios signified a real control—a reversal—of sex could not at that time be definitely decided. It was to help in making a decision as to whether the changed sex-ratios signified a real—or only an apparent—reversal of sex that I proposed in the winter of 1908–9 to carry out some chemical studies on the ova of the doves and pigeons which in Whitman's hands were yielding these striking sex ratios. The methods for the quantitative and qualitative analysis, of the very small samples to be used, were developed, and these were tested during 1909–10 on considerable numbers of the larger ova of jungle fowls and domestic fowls. Since April, 1911, I have carried on this and other lines of study to determine if possible whether the changed ratios observed by Whitman involve a real reversal of sex; this work is being actively continued.

Whitman showed that "width of cross" in doves and pigeons is of first importance in determining sex ratios and that the wider the cross the higher is the proportion of males. Family crosses produce—in practically all matings—only male offspring. Generic crosses produce from their "stronger" germs—those of spring and early summer—nearly all males. If, however, the birds of such a generic cross be made to "overwork at egg-production"—that is if their eggs are taken from them as soon as laid and given to other birds for incubation—then the same parents which in the spring threw all or nearly all male offspring may be made to produce all, or nearly all, female offspring in late summer and autumn. At the extreme end of the season eggs capable of little, then of no development, are often found in such a series. As the birds of such a mating grow older the time of appearance of females, and of eggs incapable of full development, is reached earlier and earlier in the summer or spring.

In the case of a number of hybrids Whitman showed that *color* is also affected by this pressure of reproduc-

tive overwork and season. White color could be obtained from the later, "weaker" germs, though this color did not appear in birds from the "stronger" germs of the earlier season. And further, that white, or whitened, "mutants" from pure breeds were derived almost or quite exclusively from those conditions which produce "weakened germs." Among such conditions are late season and overwork, inbreeding and great extremes of age—either very old or very young. This brief outline of Whitman's findings on sex is perhaps a more adequate, and more accurate, one than I was able to give to one of the societies represented here when I had only begun the examination of this data in 1911. Two brief summaries given on the chart (not given here) will assist in obtaining a picture of the nature of the results. I may add that by very strongly "overworking" females of some species—overworking them more strongly than Whitman did—I have been able to obtain a high predominance of females during autumn from a cross merely of *specific*² value. This result is illustrated by Chart II, though the matings there exhibited were prepared for the primary purpose of illustrating results in the study of size. It will be noted in the chart that parents overworked in a previous year throw a high proportion of females during the whole of the succeeding year, and most markedly in late autumn. In this mating the ratio at the end of the season is 14 females to 1 male; in the other (not previously overworked) there was an excess of females only after overwork—during the latter half of 1914 (7♂:10♀); and in the year following this overwork there were 21 or more females, to 11 or fewer males. Such data are not exceptional; they coincide with the usual.

Now, in the generic crosses which give all, or nearly all, males at the beginning of the season and all, or nearly all, females in the autumn what is happening?—true sex reversal? or is it selective fertilization, differential mat-

² Some data from pure breeds (pure species) mated to their own kind show also this predominance of females from late autumn under extreme overwork; such predominance is here probably less pronounced than in the case of the crosses.

uration or a selective elimination of ova in the 'ovary'? This was from the first the whole of our own problem. We have had no other, nor have we now, except in so far as the entire question of the *nature* of sex—in germ and adult—is concerned.

Our method has been to study the eggs, progeny and parents of such series as show this seasonal "reversal of the dominance" of sex from as many different angles as possible. The result till now is that we have learned some ten kinds of facts concerning the germs, or the prospective value of the germs, which issue from such a series. Let us note that these ten lines of correlated fact do not relate merely to a "normal" state of the germs, but have to do with measurable changes which occur when ova are subjected to the stress of parental reproductive overwork, which as Whitman has shown is accompanied by a shifting from male-production to female-production during the progress of the season. The diagrams of chart I will assist in making clear the nature and significance of the several correlations. The solid lines indicate a *double* correlation, *i. e.*, for both season and egg of clutch; the broken lines represent correlations established thus far for only one of these.

The generic cross that has been most fully studied involves *Turtur orientalis*—the Japanese turtle dove, and *Streptopelia alba*—the white ring dove. These species together with their reciprocal hybrids are shown (photographed) in another chart (not given here). Some data for egg size, and for sex-differences in the adult size of the several forms concerned—parents and reciprocal hybrids—are also given in that chart.

The first correlation that we have established for this series results from a study of the size of ova—*i. e.*, of yolks freed from shell and albumen. The result clearly establishes the fact that the yolks of late summer and autumn—those that produce mostly, or all, females—are larger than the yolks produced in the spring which give rise to males. And there is no jump from the one size to the other, but what may be better described as a

gradual enlargement. This fact is represented diagrammatically on chart I, and some of the actual figures may be had from the charts dealing with size of offspring (II), with analyses (III), and with calorimetry (IV).

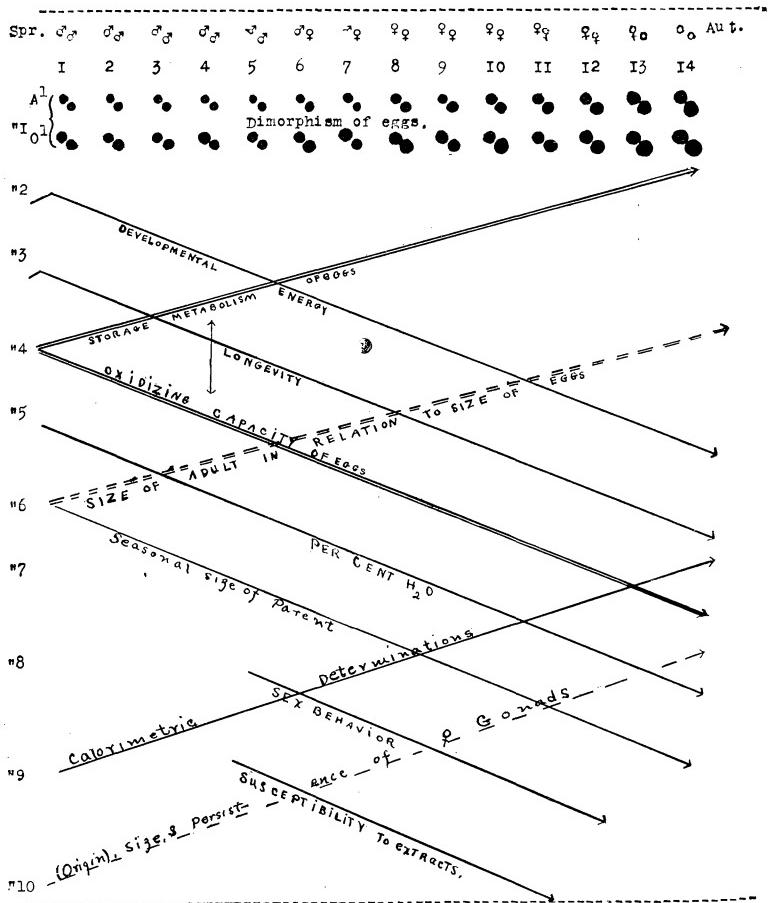


CHART I

COMPARATIVE SIZE OF EGGS OF ALBA (a) AND ORIENTALIS (o).

At the same time that this seasonal increase in size of yolks was learned, it also became evident that the eggs of doves and pigeons are *dimorphic*: That the two eggs forming the pigeon's clutch bear usually—there are exceptions—a smaller yolk in the first, and a larger yolk in the second. Since Whitman had already shown that

in the pure wild species with which he worked, males predominate in hatches from first eggs of the clutch, and females predominate in hatches from second eggs of the clutch, it became evident that the male-producing yolk is smaller—both in relation to season, and to egg of clutch, than is the female-producing yolk. Corresponding to the fact (commonly obtained from matings of individuals of the same species) that two males or two females may sometimes arise from the same clutch, we have found that a similar number of pairs of yolks of these forms are equal in size; and too that such pairs may be either large or small. The charts just referred to may be consulted in this connection. We have previously noted (1911, 1912) that in eggs laid by hybrids neither sex nor yolk-size bears the above described relations to the order of eggs in the clutch.

Still a third situation has yielded positive evidence that the smaller yolks are male-producing and the larger yolks female-producing—namely that in respect to age. It has already been mentioned that Whitman learned that the females which were “overworked” tended, when older, to begin the production of females at earlier and earlier stages of the season. Now a comparison of the size of yolks derived from younger and from older birds has conclusively shown smaller eggs for mature but younger birds, as compared with the old birds (see Chart 2). In scores of individual cases the yolk-size has now been followed from youth, and comparative youth, to old age.

In even a fourth situation it has been possible to test the relation of yolk-size to sex. Breeding data show that from the very first egg in life, and the very first egg produced after a long period of rest or inactivity, more frequently produce a *female* than do the first eggs of succeeding pairs, or clutches. Our studies on the size of such yolks show a wholly similar reversal of order of size of the two eggs of the very first clutches; the size reversals here being more frequent than in the succeeding clutches (see Chart 4).

CHART II
BREEDING RECORDS—1914

φ St. risoria 641 (old); 1913 = 42 eggs					
Series 1					
φ A1	1/1	White 140	φ T1	7/20	White 140
φ A2	1/3	White dead 2/3	σ T2	7/22	Dark 164
1st (4) = 2.066 g.		2d (4) = 2.243 g.			
H1	4/4	Inf. yolk = 1.995 g.	φ U1	7/28	White 144
H2	4/6	Inf. yolk = 2.105 g.	φ U2	7/30	White 151
φ I1	4/12 }	White killed 4/29	φ V1	8/14	White 155
φ I2	4/14 }	White 158 (?)	σ V2	8/16	Dark 169
σ J1	4/21	Dark killed 2/25	φ W1	8/22	White 152
φ J2	4/23	White 158	W2	8/24	Soft at pole
φ K1	4/29	White 147	φ X1	8/30	White 161
φ K2	5/1	White 151	φ X2	9/1	White 145
L1	5/9	Broken	σ Y1	9/9	Dark 161
L2	5/11	Dark	φ Y2	9/11	White killed
σ M1	5/18	Dark 161 (?)	φ Z1	9/18	White —
φ M2	5/20	White 163	φ Z2	9/20	White dead 10/26
φ N1	5/30	White 150	φ AA1	9/26	White 141
φ N2	6/1	White killed with ext.	φ AA2	9/28	White 146
σ O1	6/7	Dark 150	φ BB1	10/7	White 150
φ O2	6/9	White 150	φ BB2	10/9	White 144
σ P1	8/18	Dark 149	? φ CC1	10/17	Dark dead 11/8
P2	6/20	Broken	? φ CC2	10/19	White dead 11/10
φ Q1	6/28	White 143	φ DD1 }	10/26	White 130 (?)
φ Q2	6/30	White 137	φ DD2 }	10/28	White 162 (?)
φ R1	7/4	White 154	σ EE1	11/6	Dark 152
σ R2	7/6	Dark 162	φ EE2	11/8	White 143
? σ S1	7/12	Dark dead 7/29	φ FF1	11/16	White 166
? φ S2	7/14	White dead 7/31	FF2	11/18	Broken
			φ GG	11/26	White 150

1st 16 = 5 σ : 11 φ 2d 15 = 5 σ : 10 φ last 15 = 1 σ : 14 φ

The relation of the order of the eggs in the clutch to the prospective sex of the offspring is an important point, and we wish here to make this situation clear, since it seems that two rather brief statements made in 1911 and 1912, before the Society of Zoologists, have not been understood by all.

From the time of Aristotle to the present year there

CHART II—Continued
BREEDING RECORDS—1914

φ <i>St. risoria</i> 647 (young); 1913 = 18 eggs						
Series 2						
C1	2/8	Inf. yolk = 1.445 g.	φ P1	7/1	White 150	
C2	2/10	Broken	φ P2	7/3	White 15 da. emb.	
σ^{\prime} D1	3/5	Dark embr.	φ Q1	7/9	White 148	
φ D2	3/7	White	σ^{\prime} Q2	7/11	Dark 164	
σ^{\prime} E1	3/19	Dark 167	φ R1	7/22	White 152	
σ^{\prime} E2	3/21	Dark 180	σ^{\prime} R2	7/24	Dark 172	
φ F1	3/29	White 154	S1	8/3	White 13 da. emb.	
σ^{\prime} F2	3/31	Dark 190	S2	8/5	Broken 3 da. emb.	
σ^{\prime} G1	4/8	Dark killed 5/6	σ^{\prime} T1	8/12	Dark 174	
φ G2	4/10	White killed 5/3	φ T2	8/14	White 164	
φ H1	4/16	White 153	U	8/20	yolk = 1.490 g.	
φ H2	4/18	White 153	V1	9/6	"Blood circle"	
σ^{\prime} I1	4/25	Dark 169	σ^{\prime} V2	9/8	Dark 170	
φ I2	4/27	White 154	?W1	9/19	Dark dead 10/16	
J1	5/5	3-da. embr. killed	φ W2	9/21	White dead 10/14	
J2	5/7	3-da. embr. killed	σ^{\prime} X1	9/30	Dark dead 10/19	
σ^{\prime} K1	5/14	Dark 169	φ X2	10/2	White 145	
φ K2	5/16	White 158	Y1	10/29	Inf. yolk = 1.845	
σ^{\prime} L1	5/25	Dark 179	φ Y2	10/31	White 15 da. embr.	
φ L2	5/27	White 164	Z1	12/27	No dev. yolk = 1.870 g.	
σ^{\prime} M1	6/3	Dark 169	Z2	12/29	No dev. yolk = 1.925 g.	
φ M2	6/5	White 11 da. emb.	φ 641 = (170) (σ^{\prime} 170)			
σ^{\prime} N1	6/13	Dark 165	σ^{\prime} 's (5) from 1st	= 155	φ 's (13) = 149	
φ N2	6/15	White 150	σ^{\prime} 's (3) from 2d	= 165	φ 's (11) = 150	
σ^{\prime} O1	6/22	Dark killed 7/13	φ 647 = (166) (σ^{\prime} 165)			
O2	6/24	Broken	σ^{\prime} 's (7) from 1st	= 170	φ 's (5) = 151	
			σ^{\prime} 's (5) from 2d	= 175	φ 's (6) = 158	

1st 17 = 9 σ^{\prime} : 8 φ 2d 17 = 7 σ^{\prime} : 10 φ 1915 = 11 dark: 21 white

have appeared statements concerning a predominance—or a lack of predominance—of males from the first egg and of females from the second egg of the pigeon's clutch. It is unnecessary to outline these divergent reports. It is only necessary to point out the reason for discordance; though the reason we had thought to be quite obvious since 1911. The statements hitherto made have all been based on a general statistical method, which is a wholly

CHART III

SUMMARY OF PARALLEL BREEDING AND CHEMICAL STUDIES ON THE EGGS OF
 ♀ *T. orientalis* No. 500X *St. alba* No. 410 FOR THE YEAR 1912

Date	An'T's or Inc.	Wt. of Yolk	Result						
			Alc. Soluble	Phos-phatids	Protein	Ext.	Ash	H ₂ O	Energy Total
4/13									
4/15			Broken when found						
			Broken when found						
5/26	159	2.330	72.65	18.32	25.44	5.28	4.85	57.01	7,405
5/28	160	2.660	72.45	17.54	25.63	5.25	2.62	54.82	8,990
6/7	Inc.	Only one egg laid						Dark ♂
6/15	Inc.	Dark ♂
6/17	Inc.	"Very large egg"	White ♀
6/24	Inc.	No. dev.
6/26	Inc.	Dark ♂
7/3	186	2.026	72.21	16.49	26.00	3.63	2.43	56.05	6,714
7/5	187	2.330	72.27	19.18	26.55	3.75	1.93	55.22	7,881
7/15	Inc.	Dark ♂
7/17	Inc.	Dark ♂
7/23	192	2.422	72.42	17.82	25.88	3.82	1.80	55.84	8,061
7/25	193	2.720	72.45	18.88	25.96	3.86	1.81	55.33	9,296
8/2	Inc.	Dark ♂
8/4	Inc.	Dark ♂
8/13	Inc.	No. dev.
8/15	Inc.	Dark ♂
8/23	Inc.	No dev.
8/25	Inc.	White ♀
9/15	Inc.	White ♀
9/17	Inc.	White ♀
11/29	259	2.700	73.17	21.40	25.23*	55.52	9,323
12/1	260	2.715	73.02	21.63	25.38*	55.39	9,383

* Calculated.

inadequate and useless one for a study of the problem. It is now clear that the method that would be valuable for this purpose must be a thoroughly *analytical* one. Whitman has properly analyzed this situation. He has shown that normally—*i. e.*, with effects of *crossing* eliminated—from the periods for the production of the strongest germs an undue proportion of *pairs* of eggs produce males; and from the opposite period there arise undue

CHART IV

STORED ENERGY OF EGGS (1914) OF *Streptopelia risoria* (558) AS DETERMINED BY THE BOMB CALORIMETER

No.	Date	Wt. Yolk	Energy	Per Cent. Diff.
665	A1 6/6	1.010 ¹	3,358 ¹	
666	A2 6/8	0.970	3,175	-5.8 ²
674	B1 6/19	0.855	2,807	
675	B2 6/21	1.000	3,245	+15.6
699	C1 7/14	1.145	3,815?	
700	C2 7/16	1.463	5,008	+31.3?
728	D 8/30	1.395	4,812	
	E 9/9 or 10 soft shell, broken			
...	F1 10/17	" " "		
...	F2 10/19	" " "		
770	G1 11/6	1.440	4,837 (?)	
771	G2 11/8	1.720	5,797	+19.8 ?
774	H1 11/20	1.590 + sl. loss	4,906 +	
775	H2 11/22	1.780	6,015	+22.6 -
776	I1 12/1	1.640	5,614	
777	I2 12/3	1.820	6,255	+11.4
781	J1 12/12	1.535	5,302	
782	J2 12/14	1.690	5,601	+5.6
791	K1 12/23	1.485	5,266 (?)	
792	K2 12/25	1.718	5,880	+11.7 ?

¹ This egg was not only the first laid during season, but first during life of this bird.

² The percentage differences are based upon a value of 100 per cent. for the smaller egg of the pair.

numbers of pairs of eggs that produce females. To lump these all together and to count the number of males arising from first, and females from second eggs is plainly to cover up or to lose the significance of the intervening pairs of eggs which bear the significant data. Again, many matings, because of exceptional strength or of weakness, will yield a considerable total predominance of males or of females, and the statistical method lumps all these and others without thought or care of the cancellations and unsatisfied cancels involved; all of which as easily contributes to a *smoothing* of the results, as it does to a *smothering* of them.

But Whitman has also shown that not only is the *method* previously employed at fault, but that, much more important still, the *material* used—in probably all of those cases in which no correspondence of sex to the

order of the eggs of the clutch was found, and where the worker has thought it worth while to mention the *kind* of birds studied—such material has been wholly unsuitable to leading to a decision. That is to say, the “pigeons” used in these cases were one or another of the 150 *mongrels* collectively known as domestic pigeons. One of the clearest points of our present knowledge of the relation of sex to egg of clutch is that the normal relations are lost *immediately upon hybridization*—*i. e.*, in passing from the *pure state of the species*. The countless degradations and crossings suffered by the various domesticated breeds since their existence as a pure species, is therefore a sufficient index of the suitability of this material for a study of this subject. Whitman demonstrated the predominance of males from the first, and of females from the second egg of the clutch when pure species mated with pure species produce the eggs, and also the random distribution of the sexes from the eggs of hybrids. And as early as 1911 and 1912 I demonstrated charts and lantern slides which showed that the size of the yolks from pure species showed with considerable uniformity a smaller first, and a larger second yolk; and further, that this regularity breaks down at once and completely in hybrids.³

Let us now note the conclusions which follow upon the demonstrated dimorphism of the ova⁴ in the pigeons, when this is reviewed in the light of breeding data on these forms and in connection with the demonstrated relationships of size of yolk to sex—relationships which are continued even under the pressure brought by over-work, season, and age.

It becomes clear, first of all, that a selective fertilization by one kind of sperm is quite impossible—the sex

³ Note that in Chart 2, already referred to, where the eggs are produced by the female cage or blond ring dove—in which *purity* of the species is often doubtful—that a predominance of males from first, and of females from the second egg of the clutch is indicated in both series. In series I, where the two sexes arise from a single clutch, the first egg gave rise to the male in 6 (or 7?) cases; to a female in 3 cases. In series II the first egg yielded males in 9 (or 10) cases; females in only three cases.

⁴ Yolk size has now been accurately determined in about 10,000 cases.

differential residing in two kinds of eggs and not in the sperm. We may here recall that previous to our own studies, breeding data obtained from other birds had indicated that in the birds the sexually dimorphic germs are borne by the female—or to use Mendelian terms, that the female bird is heterozygous for sex.

The second conclusion that must be drawn is that a selective elimination of ova in the ovary does not occur during "overwork," while mated to a mate of another genus, nor otherwise, since the two kinds of ova are—from their size relations—positively known to present themselves under these, and under all the conditions which have been studied. In other words, the generic cross, which produces all or nearly all males in the spring, and all or nearly all females in the autumn, is utilizing in the spring a number of female-producing ova for the production of males, and in the later season is utilizing for the production of females ova one half of which had initial inclinations for the production of males. Note too that the evidence for the continued production during the season of ova of two kinds as regards sex does not rest alone on our knowledge of the dimorphic ova. For, from breeding data we learn that if the *same female* which threw all males in the spring and all females in the autumn, had been mated to one of her *own* species, then both males and females would certainly have appeared at all seasons, and largely or wholly in relation to the order of the eggs of the clutch, with but slighter effects of season to be noted. If the overwork were extreme, a predominance of females in late autumn might be expected; but in the earlier season the sexes would surely be found in nearly equal numbers. Several of the correlations soon to be mentioned, moreover, further attest that ova of two grades—in respect to sex—are produced throughout the year.

The data thus far examined exclude the possibilities of accounting for the observed sex-ratios of the generic cross on the basis of a selective action of the sperm, or of a selective elimination of ova in the ovary. What light do these data shed on the possibility of accounting

for the seasonal difference in sex-production on the basis of a differential maturation? The fact that the sperm is present in the pigeon's egg during the whole of the second maturation division may properly raise this question. On this point we must say that the particular data we have just been citing are perhaps not entirely conclusive; these data alone, however, offer the following significant points for consideration: To account for the observed sex ratios of the *generic cross* the maturation would have to be definitely differential in (1) the elimination of an X chromosome⁵ during the spring from one half of the ova, and the retention of this same X in the homologous⁶ eggs of the autumn. (2) The elimination of a Y chromosome from the other half of the eggs laid during the autumn, and the retention of all these same Y's in homologous eggs of the spring; and (3) all other chromosomes than the sex chromosomes must display no such thing as seasonal preferences for "staying" or for "going," since every observable character of the hybrids betrays the presence of both of the parental genera. This is not all, but let us pause at this point to note that even if the sex chromosomes were here capable of such wholly unknown and almost unthinkable behavior, that they have—after all—in this case wholly lost the *initiative* in governing sex, since it is the *place* in the season and the *degree* of the *pressure* of the *over-work* that has been shown to prescribe the sex of the offspring; and further, the correlations of size, water content, energy storage, etc., which we have proved to exist throughout the whole season—these correlations are all established *prior to* the formation of even the first polar body; this latter being formed only at the time of ovulation, and the second polar body forming 1 to 1½ hours after the entrance of the egg into the oviduct.

If, however, we were inclined to set no bounds to the

⁵ The chromosome situation in the germ cells of female doves and pigeons is as yet quite unknown. But whatever it may be, our statement illustrates the difficulties of a chromosome theory in the cases under consideration. We make use of a familiar case in which XY germs are male-producers, and XX germs female producers.

⁶ I. e., in eggs of identical (original) chromosomal constitution.

marvels of selective power that may be exhibited by the sex chromosomes, and to feel that even the above difficult formula remains for them a possibility, we may refer to the decisive data obtained in studies on the sex behavior of the birds which are hatched from such a sex-controlled series. We shall there see that those data differentiate *several grades of females*. Some are quite nearly males, —though they lay eggs. Is it too hazardous to suggest that in one and the same egg the Y could hardly have “gone out” to allow the egg to develop into a female, and yet have “stayed in” in order to deliver the relative masculinity that we easily detect and measure? If sex is directly the creature of a sex chromosome, the sex situation found in some of my female doves requires that the male-producing chromosome be eliminated from, and retained in, one and the same egg! The only alternative that it is within my power to imagine is that in addition to the selective elimination of the Y’s during autumn, there be further postulated a gradual fractional elimination of parts of this chromosome, larger and larger parts being eliminated during the progress of the season. Or, that the reverse of this occurs, namely that the Y, during the progress of the season, *gradually adds* something of X quality to itself, finally becoming more X than Y. For those who would value this interpretation I have no evidence or word of contradiction. The fact must always remain that our procedures have not only produced male and female from ova of opposed initial tendency—largely under control—but that several *grades of intermediate sex* have also been produced.⁷

⁷ Three previous publications, besides several addresses before the American Society of Zoologists and elsewhere, have clearly stated this result. The publications now two years since, and the citations are as follows: (a) *Carnegie Year Book*, No. 12, 1913 (p. 322), Report of Year’s Work. “The results strongly indicate that the hereditary basis of sex (and, therefore, probably all characters) is a quantitative, graduated thing; not qualitative and alternative as rather generally believed.” (b) *Science*, N. S., Vol. 39, No. 1003, Mar., 1914 (p. 440), “A Quantitative Basis of Sex as Indicated by the Sex Behavior of Doves from a Sex Controlled Series.” “These . . . results together with our very abundant data on the storage metabolism of the ova of these forms, and the initial fact of sex-control itself, strongly

We shall be able presently to note more closely the conclusive facts as to the matter of a differential maturation. Continuing our examination of the further data which we know correlate with this sort of a sex-series we shall meet with additional and other kinds of facts which lead toward a constructive view of the nature and basis of sex; facts immediate and specific concerning the measured powers or capacities of these series of ova which present us the sort of sex-series in question—facts which reveal sex in quantitative terms.

Correlations marked (2) and (3) on Chart 1 were first noted by Professor Whitman. I have been able every year to find many confirmations of his conclusions.

The curve for "Developmental Energy" on the chart indicates a progressive seasonal decrease of this capacity in the fertilized eggs; a decrease from spring to autumn. Now the evidence is unquestionable for the lowest part of the curve—the autumn. In general, least development proceeds from the last eggs of the season. These are the *largest* eggs of the year. There is also less development in the second eggs of the clutch. These are the larger of the clutch. It is thus seen that the larger the yolks the less "developmental energy" possessed by them.

The "Length of Life" of the several offspring of such a sex-series tells again of an advantage possessed by the earlier hatched birds, and of a more limited life-term affixed to the later hatches. It is further probable that within the group of clutches giving rise to females only, a longer average life-term falls to those who hatched from the first egg of the clutch, than to those arising from the second. Here, then, as in correlation no. (2) the smaller eggs of clutch and season are the eggs pro-

indicate that the basis of sex is a fluid, reversible process; that the basis of adult sexual difference is a *quantitative* rather than a *qualitative* thing." (c) *Bulletin of the American Academy of Medicine*, Vol. 15, No. 5 (October, 1914) (pp. 265-285), "The Determination of Sex and Its Experimental Control." "The sum of these results, together with the initial fact of sex control itself, practically prove that the basis of sex is a fluid, reversible process, that the basis of adult sexual difference is a *quantitative* rather than a *qualitative* thing (p. 277)," etc., etc.

ductive of "strength." The larger eggs both of clutch and season more often display "weakness." And in passing we might note that by the procedures involved in these sex-series it is possible to graduate the fatal dosage, and in great measure to predict which of particular germs must come to an end first.

The fourth kind of fact pertaining to the eggs of this series, proceeds from the results of more than 800 chemical analyses of individual eggs. The results of earlier studies of this nature were described in 1911⁸ and 1912 more fully than time limits will here permit; but the nature of these results can be noted with the help of Chart 3. It will be observed that not only does the size of the egg increase with its later position in the series, *i. e.*, with lateness of season, but the percentage of energy-yielding or stored materials increases as much as, or possibly more than, is indicated by the size—or net weight—of the yolk.

The importance, for our present purpose, of the results of these analyses is that they conclusively show (1) that the male-producing egg of the spring is an egg that stores less material than does the female-producing egg of the autumn. (2) That the male-producing egg of the clutch *stores* less material than does its female-producing mate. (3) That the eggs of old females *store* more materials, and—as has been noted—yield a higher percentage of females, than do birds not old. Therefore, it becomes evident that the egg of female-producing tendency is one whose storage metabolism is high, as compared with eggs of male-producing tendency. The analyses show that during the season successive clutches present higher and higher storage, *i. e.*, the earlier clutches store less—are more male-like; the later ones all store more—are more female-like; and as we have seen, the eggs of the low storage period give rise to males, those of the high storage period produce females. Here we obtain a close view of that upon which sex difference rests. Un-

⁸ Papers read before the American Society of Zoologists. For abstract, see *Science*, N. S., Vol. 35, pp. 462–463, March 22, 1912.

mistakably, less storage and high storage pertain respectively to the male- and female-producing germs. Unmistakably, our procedure—connected with generic cross, season and overwork—delivers males from the smaller storages in the earlier eggs. Unmistakably, these procedures raise the storage in all of the later eggs, and unfailingly we then find that these eggs yield only, or almost exclusively, females. And if we eliminate the factor of wide—or generic—cross and mate the female with one of her own species, then we see that the production of males and females coincides from the first with two sizes of eggs in the clutch—males from the smaller first, female from the larger second. Only after overwork and season have raised the storage value of the eggs, is this situation, in such a mating, seriously disturbed. And the disturbance—associated with an increase in the storage metabolism of all the eggs,—delivers, as before, an excess of female offspring.

The progressive *increase in storage capacity* of the eggs during the season—under overwork—is to be interpreted as a *decrease in the oxidizing capacity* of these same eggs. Living cells in general dispose of ingested food material by storing it, or by burning it. The products of the oxidation are removable and do not serve to increase the bulk of the cell. Likewise the low-storage capacity of the male-producing eggs as compared with the high-storage capacity of female-producing eggs is therefore an index of higher oxidizing capacity of the male-producing eggs as compared with the female-producing eggs.

The fifth correlation relates to the percentage of water in the eggs of spring and autumn, and in the two eggs of the clutch. These figures for one series of analyses are given on the chart (3) last examined. They show a higher water content for the eggs of the spring (male-producers) as compared with the eggs of autumn (female-producers); indeed, each pair of eggs from the first of the season onward has a slightly higher moisture value than the pair that follows it. The analyses further show a higher percentage of water in the first egg of the clutch

than in the second in all cases. If the results of my 800 analyses all ran as smoothly as do the 8 of this series there would be no doubt of a perfect correlation of high moisture values with small eggs, *i. e.*, with male-producing eggs—both small eggs of season, and small eggs of individual clutches. But the results are not thus uniform and smooth. There are some series which seem seriously to depart from the order noted above. These can not be discussed here. We can, however, record our own belief that the situation represented in the chart is, in the main, indicated by the moisture determinations.

Now the evidence that higher water values are associated with male-producing eggs, lower water values with female-producing eggs is of high importance in connection with our own generalization as to the basis of germinial sex-difference; and is further of much interest as being the means of demonstrating that in the—as I believe—several valid cases of sex-control now known, one thing in common has really been effected, this though the work has been carried out on a considerable variety of animals, and though the procedures have themselves been most various. The thing that seems to have been effected in all cases has been the *raising or lowering of the general metabolism of the treated germs*. If this conclusion be definitely established biology may congratulate itself that the further and complete analysis of this hereditary character lies near at hand; is open to definite and easy attack by methods already of demonstrated trustworthiness in this and other fields. And surely if such result is possible it is timely, now when the “box within box” revival has the sex character, like all others, dissociated from all *processes* that can be studied or measured, and associated with a *particle* so minute as hopelessly to defy all direct and functional investigation.

That higher water values in the tissues is associated in *development* with increased metabolism is a fact well established. We need cite here in reference to “tissue growth and repair” only the well-known fact of the higher water-content of embryonic tissues, and Minot’s calcula-

tion that in a particular mammal 99 per cent. of growth power is lost before birth. In respect to "heat production" or the "basal metabolism" of embryo and adult the data for comparison are not extensive, but it too lends support to the view that this basal metabolism is higher in the young than in the adult. It may be added that Benedict and Emmes⁹ have recently shown by very exact measurements that the basal metabolism of men is higher by about 6 per cent. than that of women.

If a higher metabolism exists in male-producing *germs*, and this is associated with higher water-content, as we concluded in 1911, it is easy to see why a number of procedures have since been shown to effect a control of the production of sex. In 1912 Miss King desiccated toads' eggs and obtained 87 per cent. of females. This was the converse of the earlier experiments of Hertwig, and of Kuschekewitch, who "over-ripened" frogs' eggs—a process during which they were found to *take up water*—and obtained, in the experiments of the latter author, as many as 100 per cent. of males. I think we can now see it was a shifting of the metabolism, through the agency of the water values, that produced the shifting of sex in the eggs of the frog and the toad.

More recently still, Whitney has effected a change in the sex of the offspring of the rotifer—*Hydatina*—a change from female- to male-production by means which he considers as serving to increase metabolism in the treated forms. Confirmation of Whitney's conclusion that it is a heightened metabolism that brings about male-production is now to be had in the result obtained by Dr. A. F. Shull¹⁰ who finds that an *increased oxygen supply* leads toward an increased production of males in *Hydatina*. It now seems clear that a *heightened metabolism* in the Rotifers is the agency of increased male-production.

⁹ Benedict, F. G., and Emmes, L. E., "A Comparison of the Basal Metabolism of Normal Men and Women," *Jour. of Biol. Chem.*, Vol. 20, No. 3, 1915.

¹⁰ Advance abstract of a paper to be presented at these meetings, December 29, 1915.

The greater production of males in cattle—indicated by Thury, Russell, and several others—from eggs that have remained unfertilized for a period of hours, is almost certainly correlated with an increased water-content which these eggs obtain before fertilization. We do not know by direct observation that the ova of the cow takes up water from the fluids that it meets in the reproductive passages. We do know that this is true for the eggs of every amphibian, reptile and bird that has been investigated. Von der Stricht has, however, described phenomena in the yolk granules of the extra-ovarian egg on one mammal—the bat—which phenomena I am quite assured from my own earlier studies on the yolk spheres, definitely indicate that in this one mammal in which the data permit a judgment, the egg does take up water from the fluid that it meets in the Fallopian tube. There is good reason to believe that the changed sex-ratios of cattle can be associated with changes in the egg-metabolism effected through, or connected with, differential water values.

The important recent work of Baltzer convincingly shows the plastic, fluid, controllable and reversible nature of sex in *Bonellia*. And, it would be difficult to believe that the larva that attaches itself to the “rüssel” of an adult, then quickly and fully differentiates, and becomes a *male*, is not displaying a higher metabolism than is the larva that rests for long in the mud and sand, and after prolonged growth becomes a *female*. Baltzer’s results deserve a much more extensive statement than can be given here.

Many points, too, in Geoffrey Smith’s illuminating studies on sex in the spider crabs would seem to be in harmony with the view that the castrated males progressively lose their initial advantages of a higher metabolism, and that they then become more female-like as they approach the lower metabolic levels which are normal to the females. Though Smith, so far as I am aware, has not thus interpreted his results.

The point to these citations is that sex control, in the several various forms in which it has been accomplished,

has been accomplished fundamentally by the same means in all—a changed metabolism, in which a higher water-content of germ and higher metabolism for male-production, and lower water-content and decreased metabolism for female production, have been definitely shown to be associated in a number of instances. Whitman learned in pigeon hybridization an additional—an entirely different—means of accomplishing the *same end* of heightening the metabolism of the germ. And, this additional means definitely tends toward male-production. The wider the cross (within the limits of the “developmental compatibilities” of the germs) the greater the vigor and strength added *by the mere act of crossing*—and at the same time the more assuredly will such crosses produce males. Even the closely related varieties used in most Mendelian crosses have not failed to indicate the greater vigor of the heterozygote.

A sixth series of studies has been made on size of the parents and offspring concerned in these sex-controlled series. Seasonal and age fluctuations in the parents, and in both sexes of both parent species; size of offspring as related to their sex, to season, and to the egg of clutch, have been studied during three and one half years. We have found no subject that presents so many complications as does the matter of the size of offspring in this series. Only a single aspect of the matter will be treated here. The seasonal fluctuation in size of the parents used in the “overworked” or sex-controlled series is, however, a simple matter. Our results show—as indicated by the lower curve on the chart (1)—that such parents weigh most in winter and spring; least in the autumn, reaching a minimum in August and September. In other words, during the period when the female parent lays her largest eggs, she herself, and her consort, are smallest in size. I have had no charts prepared showing the seasonal curves for individual birds, but data for such curves in great number are available.

Now, the single word I wish to say on the relation of size in the offspring to the order of the eggs of the clutch,

and as affected by the procedure of overwork, may be more quickly said with the aid of the charts.

One chart (only Chart 2 is reproduced here) shows the weight average of each individual hatched during the year, from two simultaneous matings of *alba* \times *risoria*. Series I is from an older pair, previously overworked; series II is from a younger pair, little—or not at all—previously overworked. It will be noted that series I is throwing large eggs, a predominance of females, and that the size of the offspring—even of the males—is prevailingly that of the *females* rather than the males of the parent species.¹¹ Series II is throwing smaller eggs, a nearly equal proportion of the sexes, except at the end of the season, and the size of the offspring is decidedly larger than in series I; and, in fact, approximates to the size of the *males* of the parent species. In both of these series it will be observed that size of offspring¹² is also correlated with the order of eggs in the clutch.

For series I, we have complete data for the year preceding and the year following the term covered by the chart. The weights for the former were: Av. for ♂'s 172 gr.; ♀'s 166 grams. For the succeeding year—early 1915—these weights are ♂'s 157 gr.; ♀'s 156 gr. Clearly, during the three-year period a change in size of offspring is progressively occurring; and the change runs from a size comparable to that of the males of the parent species, to a final size that is somewhat below that of the females of the parent species. The egg-size was known in this same series to have progressively and simultaneously changed from greater male-producing tendency to a decided female-producing tendency.

The seventh line of study intended to analyze the seasonal and clutch deliveries of the sex-controlled series is concerned with arrangements by which the sex-behavior of the birds from such series is tested. In these pro-

¹¹ The males, in both of these species, average 10–15 grams heavier than the females; the *risoria* birds are slightly larger on the average (5–10 grams) than *alba*.

¹² The weights given for individual birds represent the average of the monthly, or bi-monthly weights for the year.

cedures female is mated with female, and male with male. Such pairs—from a very few selected pairs of parents—are kept mated for a period of six months. The three and one half years that this study has been pursued has enabled us—using 30 to 50 birds—to test one and the same bird with seven others. Most of the birds used—for lack of success with the incessantly fighting males—have been females, and most of the seven successive tests with each bird have been made with its sisters of the same series. The members of the pairs are kept apart except when under observation; when put together—as they are twice daily—the records are taken of those females of the pair which behave as males in copulation with their mates. Three facts are definitely established by the data obtained: (1) The females of the *orientalis* \times *alba* cross (they are dark in color) are more male-like in their sex behavior than the females of the reciprocal cross (these are white in color). (2) Females hatched from eggs laid earlier in the season are more masculine in their sex behavior than are their own full sisters hatched later in the season. *And, several grades of females can be thus seriated according to season of hatching.* (3) The female hatched from the first egg of the clutch is more masculine than her sister hatched from the second of the clutch in a great majority of the cases. And in nearly all these latter matings the more masculine bird is so decidedly so that she takes the part of the male a full 100 per cent. of the time in copulating with her very feminine clutch-mate sister.

A fuller account of this situation was given, with the assistance of charts too large to exhibit or describe here, before the Society of Zoologists in 1913.¹³ The nature of this behavior has been adequately recorded by means of moving-picture films. Such records were also made showing the reversal of the known sex-behavior of such pairs by means of appropriate injections of ovarian and testicular extracts. Those films were demonstrated in this hall—or in one near-by—in connection with an ad-

¹³ Abstract in *Science*, March 20, 1914.

dress before the local chapter of Sigma Xi some 20 months ago.

The injection of the extracts of gonads, performed now on the third series of birds, has resulted—quite against our wish—in the death of a number of birds. In the main the deaths from ovarian injections were of the more masculine birds; while the deaths from testicular injections have been among the more, or most, feminine birds. The numbers concerned at present are not large, and a further definite study of the matter will be made before final conclusions are drawn. But the limited data now at hand indicate that the eighth correlation listed on Chart 1 is as it is exhibited there.

A ninth, and very accurate and convincing kind of information concerning the germs involved in these sex-series has been obtained by means of the bomb calorimeter. The heat of combustion of some 200 egg-yolks has been determined. One such series of determinations for 1914, in which all available eggs were burned, is shown on Chart 4. It will there be seen that the first clutch of the season bore a higher caloric value than the second, but is otherwise the smallest of the year. Beginning with the second clutch laid in June, the succeeding clutches to December 1 bear higher and higher heat values. In all clutches too, except the very first, the second eggs show a higher storage of heat units than do the first of the clutch. Here we find the conclusions reached from studies on the weights of yolk, and on yolk analyses, fully confirmed by a study of the burning value of the materials stored. And confirmed by a method in which the error involved in the determination is wholly negligible. The most accurate method, for the study of the storage values of male- and female-producing ova, gives too the results most consistent with the breeding data.

The tenth and last of these correlations deals with embryological or morphological data. It was found that some females dead at relatively advanced ages showed persistent right ovaries. The right ovary in pigeons

normally begins degeneration at or before hatching and is wholly absent from the week-old squab. It soon became evident that the persistent ovaries were found practically exclusively in birds hatched from eggs of over-worked series. Further study has shown in addition that they arise almost wholly from the eggs of autumn, and predominantly then from the second egg of the clutch—that is from eggs otherwise known to have the greatest or strongest female-producing tendency. These ovaries have sometimes weighed nearly a third as much as the adult left ovary with which they were associated, and have been found in such birds dead at all periods from a few days to fifteen months. We here attempt no adequate description of this situation, but one can not have observed the frequency of the persistence of this ovary in the birds hatched from the eggs otherwise known to be the most feminine from these overworked series without conviction that the same pressure which carries the eggs of spring from male-producing to female-producing levels, also carries the earlier female-producing level, to another yet more feminine.

In conclusion, the studies that have thus far been made on sex, and on the experimental control of sex, in pigeons go very far, we believe, toward an adequate demonstration that germs prospectively of one sex have been forced to produce an adult of the opposite sex—that germs *normally* female-producing have, under experiment, been made to develop into males; and that germs which were prospectively male-producing have been made to form female adults. That neither selective fertilization, differential maturation nor a selective elimination of ova in the ovary can account for the observed results. Further, and perhaps of more importance, these studies throw much new light on the nature of the difference between the germs of the two sexes. This difference seems to rest on modifiable metabolic levels of the germs; males arise from germs at the higher levels, females from the lower; and such basic sex differences are quantitative, rather than qualitative in kind.